# SOME QUANTITATIVE ASPECTS OF PREDATION BY MURICID SNAILS ON MUSSELS IN WASHINGTON SOUND

by
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(Plate 8)

(Work done under partial support of a National Science Foundation Grant, No. G-3298, to the Department of Zoology, University of Washington.)

The mussel-barnacle community of the rocky intertidal area offers the ecologist certain advantages for the quantitative study of trophic relationships. The greater part of the biomass of the community is incorporated in relatively few sessile or sedentary species. These dominant organisms lend themselves well to observation, sampling procedures, and experimental manipulation. The community is accessible for direct study at low tide, and under appropriate circumstances field observations may be made even during high tide. Investigations of food-web relations in any natural community provide not only information of interest in the biology of the organisms involved, but are also a step toward an understanding of the dynamics of the ecosystem in which they live.

In the summer of 1958, while at the University of Washington's Friday Harbor Laboratories, the author had the opportunity to make a pilot study of the predatory activities of three species of muricid snails, *Thais canaliculata* (Duclos), *T. lamellosa* (Gmelin), and *T. emarginata* (Deshayes), in mussel and barnacle beds of Washington Sound. The mussel beds consisted of individuals of *Mytilus edulis* Linnaeus or *M. californianus* Conrad, according to location; barnacles present were *Balanus cariosus* (Pallas), *B. glandula* Darwin, *Chthamalus dalli* Pilsbry, and perhaps *B. crenatus* Bruguiere. Since the last cannot be differentiated from *B. glandula* except by dissection, all barnacles of this type were classified as *B. glandula*, which according to Henry (1940) is the more common. The mussels and barnacles in these communities serve as the principal source of food for the three species of *Thais*. In addition the seastar *Pisaster ochraceous* (Brandt) preys upon mussels and barnacles at the lower level of the community.

Observations were made at two locations. One study area was on Turn Rock, located in San Juan Channel, east of Turn Island, at 48°32' N. lat., 122°58' W. long.; the other was on a rocky spit projecting from the north shore of Kanaka Bay, which opens from San Juan Island into Haro Strait, at 48°29' N. lat., 123°05' W. long.

Extensive beds of *Mytilus edulis* occur on Turn Rock from a tidal level of about 3.5 feet down to slightly below 0 feet. These frequently form a mat of individuals, bound together by byssal threads; the mussel bed ends rather abruptly at its lower margin. Underlying the *Mytilus* mat is a bed of living *Balanus cariosus*; this extends beyond the mussel mat to a tidal level of about -1 foot, where it likewise ends abruptly. Below the lower margin of the community a mass of broken *Mytilus* and *Balanus* shells rapidly gives way to an essentially bare, rocky substrate. *Balanus cariosus* also forms extensive beds at tidal levels above the mussel mat, with less numerous B. glandula and Chthamalus dalli occurring above mid high water. Although subjected to strong tidal currents, surf action at Turn Rock is slight, except perhaps during severe storms.

At Kanaka Bay, on the other hand, surf action is moderate to heavy. The shore is more precipitous than at Turn Rock, but the intertidal area less extensive. The same species of barnacles occur here as at Turn Rock, and the mussel on the Haro Strait side of San Juan Island is Mytilus californianus. Neither the barnacles nor M. californianus form extensive beds here; the more irregular spatial distribution is perhaps related to the broken nature of the boulder-strewn shore, which presents a substrate with varying degrees of exposure to wave action and dessication. In the shallow depressions and crevices on the more horizontal surfaces of rocks most exposed to surf action, small beds of M. californianus (15 to 30 mm. in shell length) occur. Scattered large individuals (up to 150 mm. or more) may be found in sheltered crevices and tide pools.

Thais emarginata occurs at the highest tidal levels in both study areas, at Turn Rock being most abundant above the Mytilus beds. Thais canaliculata overlaps slightly the lower part of the range of T. emarginata; at Turn Rock its distribution extends across the Mytilus beds to the lower limit of the Balanus cariosus beds which fringe the bottom of the community. Thais lamellosa is restricted to that part of the community lying below the zero tide level. At Turn Rock its range extends below the bottom margin of the mussel-barnacle community; the precipitous shore and the active surf prevented a comparable observation at Kanaka Bay. At the latter site T. lamellosa could be found higher than at Turn Rock, in shaded fissures of the upper intertidal.

Several approaches were used to obtain information about prey-predator relations in the two study areas. Observations were made of instances of predation in the field, at which time the species and size of both predator and prey were determined. Quadrat counts of predator and prey individuals were made at three tidal levels at Turn Rock, and data were obtained on size distribution of the predator population and on the Mytilus which had been killed by them. Finally, a collection was made at Turn Rock of all three species and their prey; these were brought alive to the laboratory and maintained in sea-water, where observations on predatory activity over a period of three weeks were possible. Some of the results of these various efforts will be considered.

Searches for feeding predators were made at Turn Rock on seven occasions between August 2 and 18; three such periods of search were conducted also at Kanaka Bay. Snails found on mussels and barnacles were pulled away to determine whether they had been feeding. Thais feed by drilling holes through the shells of their prey (Jensen, 1951); the presence of such a hole through a Mytilus valve, beneath the head of a snail, was considered evidence of the snail's feeding. Often the proboscis could be seen being withdrawn from such holes as the snail was pulled away.

Thirty-two instances of predation by Thais canaliculata on Mytilus edulis were observed at Turn Rock, and T. lamellosa preying on Mytilus was observed in 18 instances. Mean size of the mussel prey selected by T. canaliculata was 37 ± 1 mm. (mean ± standard error of the mean), and of those selected by T. lamellosa 32 ± 2 mm. The mean size of the mussel prey selected by T. emarginata was only 17 ± 4 mm.; this is based on five observations. Because the variance of the data for T. emarginata was significantly greater than those for the other two snails, non-parametric methods were used to determine whether the data in the three samples could be considered as having identical distributions. Using the Kruskal-Wallis one-way analysis of variance by ranks (Kruskal and Wallis, 1952; Siegel, 1956), an H value of 10.035 was obtained. Referral to the chi-square table showed this to be significant (P= .01), indicating that the distributions of the populations from which the samples were taken are not all identical. A Mann-Whitney test (Siegel, op. cit.) showed that the mussels killed by T. emarginata were significantly smaller (P= .001) than those killed by T. lamellosa. No difference was detected in the data for T. lamellosa and T. canaliculata. These results suggest that Thais canaliculata and T. lamellosa prey upon the same size class of Mytilus, while T. emarginata selects a smaller size class. Although this difference could have resulted from a sampling artifact, other evidence given below also supports the conclusion reached here. Frequency distributions of the size of mussels preyed upon by the three species are compared in Plate 8, figure 1.

Whereas dead, drilled Mytilus edulis shells, which were still attached by their byssal threads, were extremely common at Turn Rock, at Kanaka Bay only ten drilled M. californianus shells were found in the entire research area. The latter had been washed up on the beach. Probably surf action breaks free dead shells at Kanaka Bay, so that they do not remain as evidence of predatory activity. No Thais was seen on beds of small Mytilus located on exposed horizontal or gently sloping surfaces of rocks at Kanaka Bay, nor was any observed on the scattered large individuals of Mytilus occurring in the more protected areas. It is suggested that surf action may prevent predation by Thais on these exposed surfaces, since generally these snails were not found in such areas. Perhaps in the more protected areas the snail population eliminates most of the mussels, with only a few escaping predation until large enough no longer to be subject to attack by Thais. Observations to corroborate or negate this hypothesis are needed.

On barnacles, evidence of predation was considered established if a hole drilled through the parapet was apparent when a snail was pulled away from a barnacle, or if the scutal plates remained gaping after the snail was pulled away. Often the proboscis could be seen being withdrawn from between the scutal plates as the snail was removed. At Turn Rock all three species of Thais were found preying on Balanus cariosus as well as on Mytilus edulis, although both T. canaliculata and T. lamellosa appeared to prey primarily on the mussel. Thais emarginata, on the other hand, was found preying more often on barnacles than on mussels, and on both B. cariosus and B. glandula. At Kanaka Bay T. canaliculata and T. lamellosa were found preying on B. cariosus, and T. emarginata on B. cariosus and Chthamalus dalli.

Observations were made during high water at Turn Rock on August 9 and 10, using a glass-bottomed underwater viewer. Numerous Thais emarginata were seen scattered over the barnacle beds; it is not unlikely that many of these were feeding. Thais canaliculata were abundant on exposed, higher Mytilus beds where, during low water, they were not present. Since drilled Mytilus shells were common on the higher Mytilus beds, and Thais canaliculata could be found aggregated there in crevices during low water, it appears that on these more exposed mussel beds Thais canaliculata does most of its feeding during low water. In the lower beds, which remain moist during low water, it could be found feeding when exposed by the tide. Pisaster ochraceous could be seen during high water at the lower margin of the community; they did not move up onto the barnacle or mussel beds.

On August 13 counts were made of mussels, barnacles, and snails in eight 25 cm. square quadrats at Turn Rock. Three counts were taken below the zero tide level, just above the lower edge of the mussel bed; two were made in the center of the mussel bed, and three were made in the higher barnacle bed. At each level the sites of the separate counts were determined by tossing the quadrat marker. In each quadrat snails were identified and the length of their shells measured, and living mussels and barnacles were counted in situ; dead mussel shells were collected and taken to the laboratory for measurement and examination for holes drilled by Thais.

A total of 145 dead, drilled Mytilus shells was taken in the quadrat counts at Turn Rock, representing 24% of the total number of mussels in the quadrats. Size distribution of these drilled shells is shown in Plate 8, figure 2. The mean size of this sample was 27 ± 1 mm. This is significantly smaller (using the t-test; P = .005) than the mean of 31 ± 1 mm. for the total of Mytilus in the predation observation samples from the same area. It should be noted that the mean size of the Thais canaliculata in the sample taken from the quadrat counts was 23 ± 1 mm. This is significantly smaller (P = .005) than the mean of 29 ± 1 mm. for those in the predation observation sample. Similarly, the mean size of Thais lamellosa from the quadrat counts, which was 37 ± 2 mm., is significantly smaller (P = .005) than the mean of 47 ± 2 mm. for those taken in the predation observation sample. These differences are due, undoubtedly, to a sampling bias made in the predation observations. Perhaps, then, the mean size of Mytilus from the predation observation sample is greater than that from the quadrat counts because of a positive correlation in size of prey and size of predator. To test this, correlation coefficients were calculated for the size of both species of snails and their Mytilus prey, but neither differed significantly from zero. Some other explanation seems likely, therefore. Since the dead mussels collected at Turn Rock were drilled at some unknown time in the past, the smaller mean for this sample may be due to presence in the sample of shells drilled when the population was much younger. On the other hand, the difference may reflect the inclusion in the sample of numerous mussels killed by T. emarginata, which we have seen appears to select smaller mussels than do the other two species. Only five Mytilus killed by Thais emarginata were included in the data from the predation observation sample. Additional evidence supporting the second suggestion will be developed below.

A collection of mussel and barnacle covered rocks, portions of the mussel mat, and representatives of all three species of snail predators was made at Turn Rock on August 2. The material was taken to the laboratory and placed in a glass-fronted outdoor tank supplied with running seawater. Thirty-four

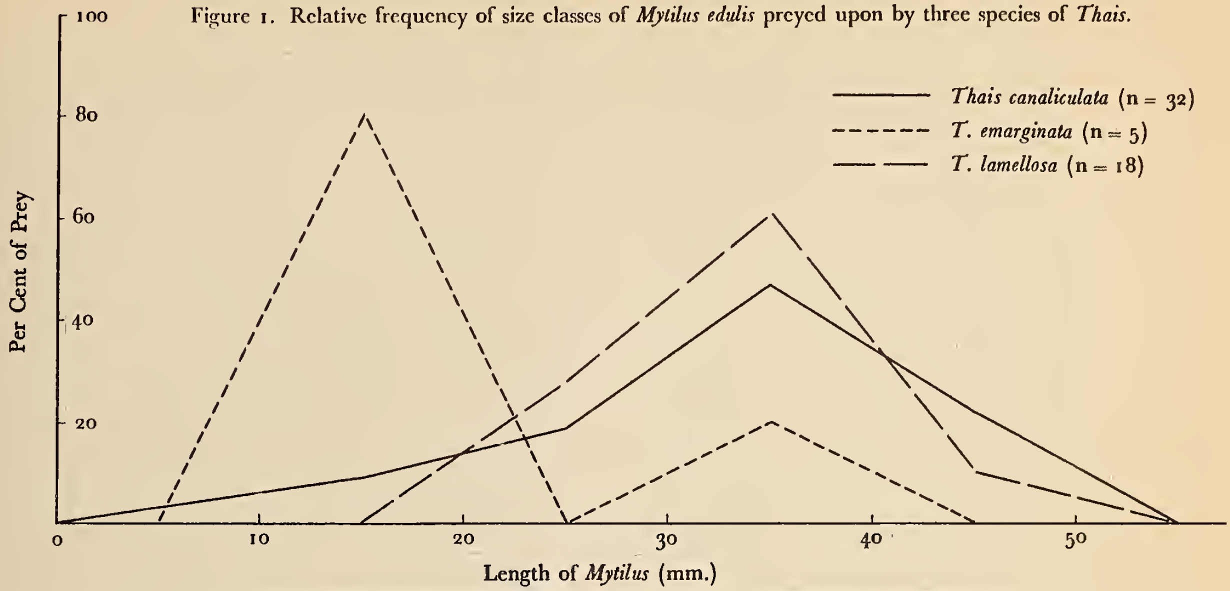


Figure 1. Relative frequency of size classes of *Mytilus edulis* preyed upon by three species of *Thais*.

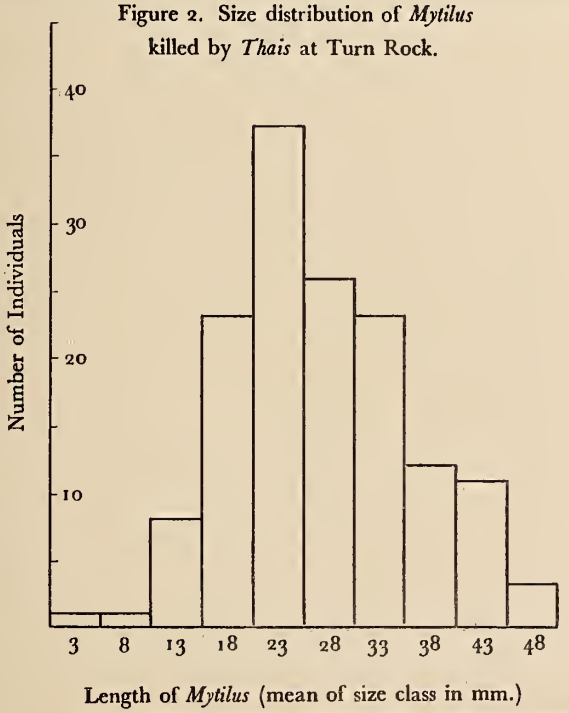


Figure 2. Size distribution of *Mytilus* killed by *Thais* at Turn Rock.

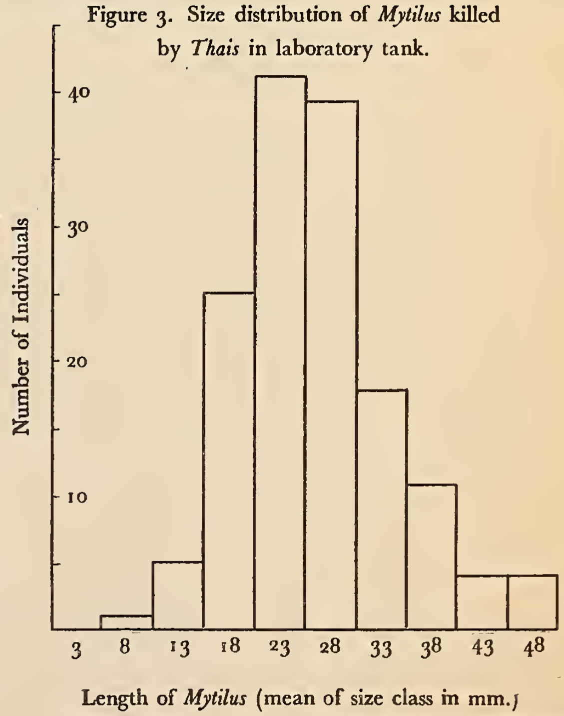


Figure 3. Size distribution of *Mytilus* killed by *Thais* in laboratory tank.

snails, including some of each species, were marked with numerals of red enamel. Subsequently, observations were made two or more times daily, and a notation was made when a snail appeared to be feeding. When a particular snail moved, after having been stationary on a particular mussel or barnacle during two or more consecutive observations, the mussel or barnacle was examined to determine whether it had been preyed upon by the snail. In addition, the aggregates of *Mytilus* in the tank were examined on August 6 and all dead shells removed.

Twenty days following removal of the original dead *Mytilus* from the tank, all drilled, dead *Mytilus* were again removed. They numbered 145. A histogram of their size distribution is shown in Plate 8, figure 3. It is similar to that for the 145 drilled shells taken in the Turn Rock quadrat counts (equal numbers being a coincidence). The mean size of drilled *Mytilus* from the laboratory tank was 26 ± 1 mm., which does not differ significantly from the mean of 27 ± 1 mm. from the quadrat counts. The mean from the laboratory tank differs significantly from that for the predation sample ($P = .005$), as does the mean from the quadrat counts (see above). Two explanations may be suggested for these results. On the one hand, it is possible that the small mean size of killed *Mytilus* from the laboratory tank indicates, that, inadvertently, the mussels brought to the laboratory were smaller on the average than those in the field population from which they were taken. On the other hand, the mean of the predation observation sample may be larger than that from the laboratory tank, as well as that from the quadrat counts, because it reflects little influence of small *Mytilus* killed by *Thais emarginata*. The similarity of size distribution of drilled *Mytilus* from quadrats and tank can be taken to suggest that similar size classes were available in the tank and on Turn Rock. It would appear, for this reason, that the second suggestion is supported more strongly by the evidence.

In 24 observations of predation in the laboratory tank a record was kept of the length of time spent by marked predators on their prey. Eighteen of these fell in a 24 to 48 hour range. One snail remained on its prey 56 hours, and two almost 70 hours. Three persisted only four hours; these animals may have been interrupted before completion of the feeding process. Apparently the length of time usually required for a snail to complete drilling and feeding is on the order of one to two days. No differences in feeding time were detected for different species of predator, nor for different species of prey.

From the observations made in the laboratory tank, it is possible to calculate a very speculative, but nonetheless interesting, feeding rate of *Thais canaliculata* on *Mytilus edulis*. Of 28 feeding observations in which *Mytilus* was the prey, 22 involved *T. canaliculata* as predator. If it may be assumed from this that 80% of the 145 *Mytilus* killed during the 20-day period were preyed upon by *T. canaliculata*, we compute that 116 of the dead *Mytilus* were attacked by snails of this species. Present in the tank during the period were 43 individual *T. canaliculata*. On the basis of this, a feeding rate of 0.13 mussels/snail/day was computed. For comparison, Hanks (1957) found that *Urosalpinx cinerea* (Say) fed on 10 to 30 mm. long *Mytilus edulis* at the rate of 0.24 mussels/oyster-drill/week, or 0.034 per day. Connel (in press) reported that *Thais lapillus* (Linnaeus) fed on *Balanus balanoides* (Linnaeus) at Millport at the rate of 1.0 to 1.3 per day in the summer and 0.4 per day during the winter.